PALMEN'S ORGAN AND ITS FUNCTION IN NYMPHS OF THE EPHEMERIDÆ, HEPTAGENIA INTERPUNCTATA (SAY) AND ECDYURUS MACULIPENNIS (WALSH).

J. E. WODSEDALEK.

Introductory Remarks.

Our knowledge concerning the tracheal system in the Ephemeridæ dates back to the time of Swammerdamm (1752), but the existence of this interesting modification, Palmen's organ, found only in the tracheal system of this group of insects, was not known until comparatively recent times. Swammerdamm in his "Bibel der Natur" gives a large figure (Plate XIV.), showing in some detail the internal anatomy of a may-fly nymph, but the Palmen's organ and even the four tracheal tubes directly leading to it, if present in that species, apparently escaped his observation. This omission was no doubt due to an imperfect dissection; for, upon closely observing his representation of the air tubes in the head of the nymph he figures, one can detect a single projection leading from the main tracheal tube on the left, which corresponds somewhat to one of the four tubes normally leading to this organ; the other three tubes and the organ itself were doubtless destroyed in his preparation, and hence not represented in his figure.

The presence of this chitinous structure was first noted by Dr. J. A. Palmen (1877), after whom the organ is named, and in his work he says: "Die vier im Scheitel zusammenstossenden Aeste bilden in ihrem Kreuzpunkt einen rundlichen, aus concentrischen Chitinschichten bestehenden Körper, dessen Bedeutung ich nicht kenne." On Plate I. (Fig. 7) he gives a figure of the head and thorax of the nymph of *Cloëon dipterum* L., showing the location of this organ in its relation to the four tracheal tubes of the head, without making any attempt to describe it. He makes the statement that the tracheal system is essentially the

same in the twenty-three species which he examined. It is not entirely safe, however, to infer from this that the prominence of Palmen's organ is essentially similar in these various species.

The species upon which the present study is based are *Heptagenia interpunctata* and *Ecdyurus maculipennis*. These two forms are very closely allied, not only in matters concerning this organ, but also in their natural habits and general behavior, and the present paper will concern itself with nymphs of *H. interpunctata*, unless otherwise specified.

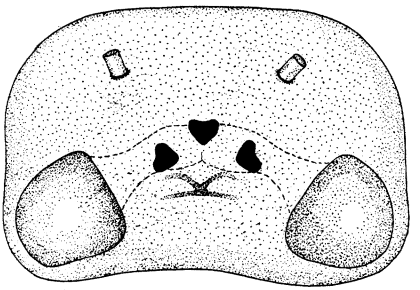

FIG. A. Head of *H. interpunctata* nymph. Basal joint of antennæ only drawn. The brain is drawn, dotted, under the three ocelli just posterior to which is shown the Palmen's organ and the four tracheal tubes leading into it.

Fig. A shows the relative position of the organs in the head of a nymph. Palmen's organ together with the tracheal tubes leading to it can be readily seen through the chitinous covering, especially in the newly moulted specimens, by placing them under a binocular. It is symmetrically located between the two large compound eyes and a little posterior to the brain. Fig. 1 shows the organ in its relation to the entire tracheal system of the head. It has been the fortune of the writer to be able to make a perfect dissection of the system, the first time merely through an accident. Upon placing a specimen which had been dead for some time under a binocular almost the entire tracheal system of the insect became visible through the transparent chitinous covering. The muscles and all the other soft tissues had sufficiently decomposed to form a sort of liquid mass. The thin hypodermal walls surrounding the air tubes too had disintegrated, and practically all that remained in good condition was the exoskeleton and its internal continuation, the tracheal system. The location

and arrangement of the more important parts of the system were carefully noted and a diagram indicating the relative position of the main tubes was sketched. The external covering was carefully broken between the pro- and mesothorax and a gentle pull on the anterior edge of the head removed it, fully exposing the air tubes which remained in position. The macerated mass was carefully washed off and the tracheal system being completely filled with air presented the most beautiful silvery effect against a dark back-ground. Even the very finest branches remained, but no attempt was made to include them in the figure.

Description of Palmen's Organ.

Gross (1903) attempts to describe the organ in considerable detail; this description and his ideas in general are not fully corroborated by the results of my studies. He says in part: "Reconstruiren wir jetzt aus den besprochenen Schnittbildern das ganze Organ, so erhalten wir folgendes Gesammtbild. Ein Körper, der im Längsschnitt kurz elliptisch, im Quersschnitt ungerfähr kreisförmig ist, setzt sich aus 14 concentrischen, aus zartem Chitin bestehenden Schalen Zusammen, die an ihrer Innenfläche mit feinen Härchen dicht besetzt sind. Das Ellipsoid ist aber kein vollkommen geschlossenes. Vielmehr ist es von vier Seiten her [sehr] tief ausgehöhlt. Das ganze ist in den Kreuzungspunkt von 4 im Scheitel des Hinterkopfs zusammentreffenden Tracheenästen eingeschaltet, und zwar so, dass die Luft zwischen den Schalen frei circuliren kann, wenn auch durch die grosse Zahl der Härchen einigermaassen behindert. Ganz ähnlich gestaltet wie bei *Ephemera vulgata* L. fand ich das Palmen'sche Organ noch bei *Baëtis rhodani* Pict., *Heptagenia sulphurea* Müll., ferner bei den Larven einer *Caënis* sp. und einer *Chirotonetes* sp. Einige geringe Abweichungen in der Gestalt bei *Baëtis rhodani* konnte ich nicht hinreichend genau feststellen, un sie hier zu besprechen, da ich mir nicht genügend Material beschaffen konnte."

The Palmen's organ in both *H. interpunctata* and *E. maculipennis*, is not composed of concentric shells nor are there any hairs present on the inner surface of the scales which Gross describes and pictures in allied species. Well prepared slides

of cross sections show that the organ is not perforated with air passages but is a continuous mass of chitin in which the differentiations are due mainly to variation in density of color. Sections of adult specimens were also made and carefully examined, but no difference in the structure of the organ could be detected. Dr. Gross has no doubt mistaken the clearer areas or concentric layers for air passages and the darker layers for separate solid areas forming the scales from which the hairs protrude.

Fig. 4 shows the external dorsal appearance of the organ and its relation to the four tracheal tubes, the entire structure being enveloped by the hypodermal layer; Fig. 5 is a horizontal section of the same. The description of the organ can be best understood by studying it in connection with its development and growth. It is a well understood fact that the tracheal system in insects is formed by the invagination of the ectodermal layer. As to the origin of Palmen's organ I am not at all certain for embryonic material has thus far in this study not been available. The appearance of the structure of the central portion of the organ suggests that, during the process of the development of the tracheal system, the four large tubes leading to the organ (Fig. 1) come together at a common point; here the blunt ends of the invaginated portions, the tracheæ, surrounded by the hypodermis, fuse and secrete this common center. From the various cross sections of which Fig. 8 is typical, it can be inferred that the two posterior tubes come together first and that a portion of the center is secreted before it is met by the two anterior tubes.

In the many sections of *H. interpunctata* and *E. maculipennis*, which were examined, the center of the organ does not show any ring-like structure, but is an irregular mass which is apparently secreted before the larva casts the first lining of its tracheal system. At the time of this first ecdysis which is accompanied by the shedding of the inner lining of the air tubes, this central mass is larger than the openings in any of the four tubes and hence the impossibility of its being cast out of the body. Shortly after the casting of the inner lining of the tracheæ, the hypodermal cells surrounding the tubes undoubtedly begin to secrete the new chitinous wall. The hypodermal layer surrounding the central mass, the beginning of the Palmen's organ, is continuous

with the layer surrounding the air tubes and apparently begins active secretion at about the same time. The different conspicuous rings which are shown (Figs. 5–9) are sections through the concentric layers of the organ and are directly correlated with the various moults. Further evidence of this correlation is obvious from the fact that the number of rings is directly in proportion to the size of the insects themselves. An examination of the sections figured shows that the hypodermal cells surrounding the organ are much larger than those enclosing the tracheæ, and hence, the greater the secretion of these larger cells; from this results the greater thickness of the chitinous layers of the organ as compared with that of their continuations, the walls of the tracheal tubes. Coincident with this increase of volume of the organ, the cells surrounding it must necessarily multiply as they are pushed outward. Thus, by means of successive periodic secretions the Palmen's organ is built up; the old layers of the organ are not cast off as are the walls of the tracheal system, with which they are continuous.

Gross in commenting on the function of Palmen's organ says: "Ich glaube deshalb, dass für das räthselhafte Organ keine Erklärung gefunden werden kann ohne Berücksichtigung des Nerven. Nehmen wir aber an, dass dieser wirklich zu dem Organ gehört, so kann dieses nichts anderes sein als ein Sinnesorgan. Da es aber, wenn auch ziemlich direct unter der Hypodermis—von dieser nur durch wenig Fettkörper getrennt—doch jeden Falls im Innern des Körpers der Thiere gelegen ist, kann es von allen uns von andern Thiergruppen bekannten Sinnesfunctionen nur denen eines Gleichgewichtssinnes dienen." Up to the present study no experimental work on the organ has been attempted with the view of obtaining evidence as regards its function. Gross also says: "Man könnte meinen, der Beweis für die Richtigkeit der von mir versuchten Deutung des Organs liesse sich vielleicht durch zweckmässig angestellte Versuche erbringen. Das erscheint mir aber ziemlich aussichtslos. Es wäre ja gewiss nicht unmöglich, das recht oberflächlich gelegene Organ zu zerstören, nachdem man vorher seine Lage so genau festgestellt hat, dass man sie schon von aussen am lebenden Thier angeben kann. Aber ich fürchte, dieses Experiment wird nicht viel helfen. Stellt

sich nach dem operativen Eingriff irgend eine Aenderung der Flugweise ein, so kann diese auch durch die Verletzung an und für sich bewirkt sein. Wir wissen aus der experimentellen Gehirnphysiologie der Vertebraten zur Genüge, in welche schwere Irrthümer man geraten kann, wenn man die Verletzung oder Zerstörung eines Organs oder Organtheils als reinen Versuch betrachtet. Während man aber bei einem Wirbelthier wohl warten kann, bis die störenden Nebeneffecte des operativen Eingriffs verschwunden sind, so scheint mir das bein einer 'Eintagsfliege' kaum möglich zu sein. Selbst ein nicht zur Begaltung gelangtes Exemplar dürfte in der Gefangenschaft nur zu bald eingehen. Auch würden die Thiere wohl kaum den Hochzeitsflug aufnehmen, wenn man sie nicht in die ihnen zusagende, natürliche Umgebung und unter Artgenossen bringt. Thut man dies aber, so würden einem die Versuchsthiere gar zu leicht entschlüpfen, nachdem sie einmal aufgestiegen sind. Ebenso wenig Erfolg verspreche ich mir von dem Versuch, die Function des Organs durch Verkleben der in die Kopftracheen führenden Stigmen festzustellen."

Removal of the Organ.

Experimental work on the removal of the organ did, as Gross said, at first seem impossible. It is needless to say that the task was very tedious and at the outset far from encouraging, this was mainly due to the small size of the organ and its close proximity to the brain. At first the cauterizing method was used but without satisfactory results, then two very fine platinum needles which were attached to the two wires leading from a galvanic battery were employed. The apparatus was provided with a resistance box so that the voltage could be varied at will. In this method the end of one needle was turned into a small loop through which the sharp point of the other was inserted, thereby completing the current, heating the sharp point intended for the operation, and at the same time, greatly facilitating the necessary steady manipulation of the outfit. The hot point of the needle would be brought directly over the organ and then a rapid insertion and withdrawal of the point of contact followed. It was impossible at each attempt to destroy the organ owing

to its natural instability. A few specimens from which the organ had been thus entirely removed, lived a sufficient length of time to enable studies of the behavior of the individuals, and of the regeneration of some of the destroyed parts.

Becoming more thoroughly familiar with the structure and exact position of the organ in its relation to the vital parts of the head, a more simple method was devised. By means of two very fine and sharp-pointed needles a small slit can be made through the chitin above the organ and then, inserting a needle at each side between the posterior and anterior tracheal tubes leading to the organ, it can with some practice, be entirely removed; this treatment apparently causes the insects but little pain. The four tracheal tubes were usually separated near the organ though sometimes they would break off near their juncture with the main longitudinal tracheæ. In special cases, for studies of regeneration of the organ, the four tubes were broken off at their immediate attachment to the organ or at various definite distances from it. This was possible by pressing the two points of the needles on either side of the place where the break was desired. Bleeding was very rare and usually the edges of the chitinous slit were brought so close together that the detection of the wound was rendered almost impossible.

After treatment by this method the activity of the nymphs when placed back into the water did not seem to be impaired by the operation, and the wounds healed over within a few days. By this method not only was the removal of the organ assured, but mortality was reduced to a minimum. In one set of experiments forty-nine out of fifty specimens operated on lived for more than two months after the operation. It might be said in this connection that no regeneration of the organ takes place. The ends of the broken tubes heal over within two or three weeks and with the exception of a few small air tubes which grow out from the blunt ends of the four tubes, during the same time, no further growth was observed in any of the specimens as long as four months after the organs had been removed. Fig. 3 is drawn from a nymph in which the tracheæ were broken off at their point of contact with Palmen's organ, they almost touched but no regeneration of the organ

took place, nor was there a union formed between the different tracheæ Fig. 2 is of a specimen in which the tracheæ were broken at quite a distance from the organ; again, no growth beyond the covering over of the broken ends and the formation of a few small tubules took place.

Comparison of the Behavior of Normal and Operated Specimens in Relation to the Function of Palmen's Organ.

In my previous papers (Wodsedalek, '11 and '12), the behavior of *H. interpunctata* nymphs has been discussed in considerable detail, and hence only the more important phases of the behavior of this insect which directly concern this problem will be cited here. The nymphs are decidedly negative in their phototactic response in all gradations of light, varying from ordinary daylight to very intense electric illumination. Their thigmotactic propensity, or tendency to come in contact with and cling to objects, is especially pronounced. In their natural environment the nymphs are never seen swimming freely about in the water, even when observed in their favorite places in which they occur in great abundance. In their natural habitat they are always found clinging to the under surfaces of small rocks, and this same position is regularly assumed by all normal ones in the aquaria of the laboratory. When a stone, to which the specimens are attached is inverted in the water, the insects soon make for its under side, many of them doing this as the stone is being turned over. This is also true of normal specimens in the dark-room, and hence it is obvious that this tendency of the nymphs to cling to the lower surfaces of rocks, with their dorsal side downward, is not due entirely to their negative reaction to light. It is unquestionably due, in part, to a definite power of orientation independent of phototaxis.

Specimens from which the Palmen's organ was removed react to light in practically the same way as do the normal specimens. Their thigmotactic inclinations, too, do not seem to be impaired. However, when the insects are taken into a very shaded or a dark-room the difference in orientation becomes quite obvious. When a stone to which the insects are attached is

inverted in the water, or when the specimens are dropped on a stone in the water in a dark-room they remain on the upper surface or on the sides of the rock for a considerably longer time than do the normal individuals By the removal of the organ the nymphs have no doubt lost, to some extent, their usual keen sense of orientation, for under such conditions they would be seen on the top, sides or any part of the rock for hours, days, and even weeks after the operation had been performed. The same was true of every lot experimented with. It was also noticed, with several lots of operated specimens, that the tendency to remain on almost any part of the stone was gradually diminished and that after several weeks and in some cases about two months there were comparatively few individuals to be seen on the upper surface, regardless of the fact that in some special experiments the stone would be inverted at every observation with the view of bringing more specimens to the upper surface with little disturbance. This growing partiality to the lower surface of the stone does not lessen the significance of their former behavior, for, from my studies on the power of the formation of associations in the nymphs of *H. interpunctata* (Wodsedalek, '12) it was found that they gradually formed several types of associations. The associations formed in these experiments were in connection with their thigmotactic inclinations, which were in great part responsible for the gradual decrease of the number seen on top, and the gradual diminishing of the time the various individuals required to retreat to the lower surface.

In another paper (Wodsedalek, '12) on the natural history and general behavior of these insects I have discussed their thigmotaxis in considerable detail. It was learned from a simple experiment that their thigmotactic propensities are best satisfied when their dorsal as well as their ventral surfaces are in contact with some object. "When several specimens are placed in an aquarium they mass together into clusters where they remain for hours, and if recently collected, even days. As soon as a rock or any other object is placed in the water the loose forms swim toward it, while considerable time often elapses before the masses are broken up. Two long bricks were placed one over the other in a basin of water and between them were placed small pebbles

varying in size so that the space gradually varied in thickness from one end to the other. Then a large number of specimens were put in the water and after a short time it was found that nearly all of the specimens were attached to the lower surface of the upper brick with their dorsal sides downward, and a large majority of the specimens were in that part of the wedge-shaped space where their backs came in contact with the brick below." The operated specimens in their wandering about over the surface of the stone accidently came into such a place where their backs came in contact with the floor of the basin. This stimulus naturally appealed to their thigmotactic propensity and hence the greater tendency to remain on that portion of the rock. It seems only natural, therefore, that an association would be formed between this more satisfactory environment and the lower surface of the stone. It is not altogether improbable however, that such a habit had already been partially formed before the operation took place.

Further evidence for the fact that this thigmotaxis is largely responsible for the gradual disappearance of the insects from the upper surface, is apparent from the results obtained in some checking experiments. In those experiments the stone was suspended in the water so that the backs of the nymphs could not come in contact with other objects. The results were surprising and all remaining doubts as to the function of the Palmen's organ in the nymphs were resolved. As long as the experiment was continued the specimens remained quite evenly scattered over the entire surface of the suspended stone. A similar experiment was tried with the normal specimens, also in the dark chamber, and practically all of the specimens remained exclusively on the lower surface. It is only natural, then, to conclude that Palmen's organ has a great deal to do with the orientation of these insects. That this unusual behavior is not due to the shock the insects receive from the operation was proven by the fact that when other parts of the head and body were destroyed no comparable results in behavior took place.

Although the foregoing results are thoroughly convincing as to the function of the organ in these nymphs, further results of observations on behavior relative to the rôle of the organ may

be cited. When the specimens are collected and dropped into a dish of water many of the individuals fall to the bottom with their ventral sides upward. This toppling over is even more obvious when the specimens are placed in a dish of water near a light. In their attempts to get away from the light and repeatedly clawing at the opposite end of the dish the specimens become exhausted and very frequently when the clawing movements cease the apparently lifeless individuals fall to the bottom, dorsal side downward. This period of rest corresponds somewhat to the death-feigning instinct of the insect. By vigorously stirring up the specimens or throwing them into water having a temperature to which the specimens are not accustomed, or into relatively strong chemical solutions of various sorts, as acids, salts, alcohol, etc., practically all of the specimens fall into this momentary, rather stiff, inactive state and slowly descend to the bottom of the dish. In so doing almost all of the specimens topple over and fall down head-first, ventral side up and on the average, at an angle of about 45 degrees. It might also be mentioned here that nymphs which are found dead in the aquaria lie almost invariably with their ventral side up. On the other hand, the turning over is under similar conditions far less frequent among the specimens from which the organ had been removed. If two groups of freshly killed specimens are taken, all of which have been cleaned and their appendages arranged, the one group normal in every way, the other having the Palmen's organ removed, we find by allowing them to descend through a deep jar of water that almost invariably the former topple over and settle on the bottom ventral side up, while the latter equally as frequently reach the bottom and remain there with their ventral side downward.

Concluding Remarks.

The results of the foregoing experiments show conclusively that the organ, as small as it is, plays a very important rôle in the behavior of the nymphs upon which these experiments were performed. This is doubtless due to the weight of the chitinous mass whose pressure seems, to a large extent, to control certain orientation of the insects. Gross (1903) gives a figure of the

cross section of the head of a may-fly showing the position of Palmen's organ in relation to the other parts, and in his discussion says,—"Unter dem Palmén'schen Organ verläuft nämlich bei allen 5 von mir untersuchten Ephemeridenspecies ein starker, vom Gehirn kommender Nervenstrang. Seine Lagebeziehungen ergeben sich aus Fig. B, die einen Medianschnitt durch den Kopf einer Ephemera vulgata bei schwacher Vergrösserung darstellt. Der erwahnte Nerv (*np*) verlauft in der Medianlinie vom Gehirn (*g*) nach hinten unter dem Palmén'schen Organ (*p*) hindurch und heftet sich hinter ihm an der Körperwand an. In einem Theil seines Verläufs liegt er direct auf dem Nervus recurrens (*nr*) des unpaaren sympathischen Nervensystems."

Careful examination of many nymphs showed no evidence of the presence of the two large nerves which Gross speaks of as present in the imaginal species which he examined; this was also true of the adult specimens which I examined. It appears from his discussion of the subject and from his figure (page 98), that what he speaks of as nerves may possibly be the two muscles which play an important part in the movement of the head. The posterior attachment of these muscles to the exoskeleton evidently corresponds to the attachment of the large nerves he misrepresents. In my preparations very thin sections were made, but no signs of nerves extending directly from the brain to the organ were detected. Taking the structure and function of the organ into consideration we should not expect the presence of such nerves. A mass of rather loose tissue exists between the organ and the brain, and the two are loosely united by means of connective tissue. It is the writer's opinion that the chitinous organ being so loosely supported by the four tracheal tubes exerts a pressure on the surrounding tissues, whereby the disturbing stimulus reaches the central nervous system. The observations mentioned on the descent of nymphs in various conditions, through the water, particularly the death-feigning and the dead individuals, seems to indicate that the orientation is also, in part, a self-directing process, that is, by the presence of the organ the nymph is swerved into position—a matter of physical equilibrium.

Gross' theory that the organ functions only in the adult speci-

mens seems quite untenable. Aside from the results of my experimental work arises another question. Why should this structure occur and persist in very small nymphs, and grow in relative proportion during the comparatively long nymphal stage of two, and in some cases three years, for the purpose of becoming functional only after the nymph metamorphoses into its short-lived adult stage, when all the other modifications which are of a direct advantage to the adults develop during the comparatively short time immediately preceding the transformation?

The extent of the functions of this organ in the adults thus far remains unknown. Miall (1895) in speaking of the Ephemeridæ gives the following quotation: "The recently emerged fly," says De Geer, "settles on trees, plants, walls, etc., near the water which harbored the larva. Here it fixes itself by the hooks of the feet, usually with the head downwards, and rests until the last or sub-imaginal moult is at hand." My observations of the behavior of adult may-flies are to some extent in accord with those of De Geer, however, no theory as to the probable function of the organ in the adults can be propounded, unless it can be supported by reliable results of experimental work. A large number of nearly full grown nymphs from which the Palmen's organ had been removed are now in the aquaria with the view of making a study of their behavior, when they emerge as adults in comparison with that of the normal individuals.

Among the twenty-three species in which Palmen (1877) noted the presence of this organ, there are several free swimming forms, and at this time, it is difficult to say just what part Palmen's organ plays in those forms during their life history as very little is known of their natural habits.

I am greatly indebted to Professor William S. Marshall for suggesting this problem, and also, for his help and earnest interest in the progress of the work.

ZOÖLOGICAL LABORATORY,
UNIVERSITY OF WISCONSIN.

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EXPLANATION OF FIGURES.

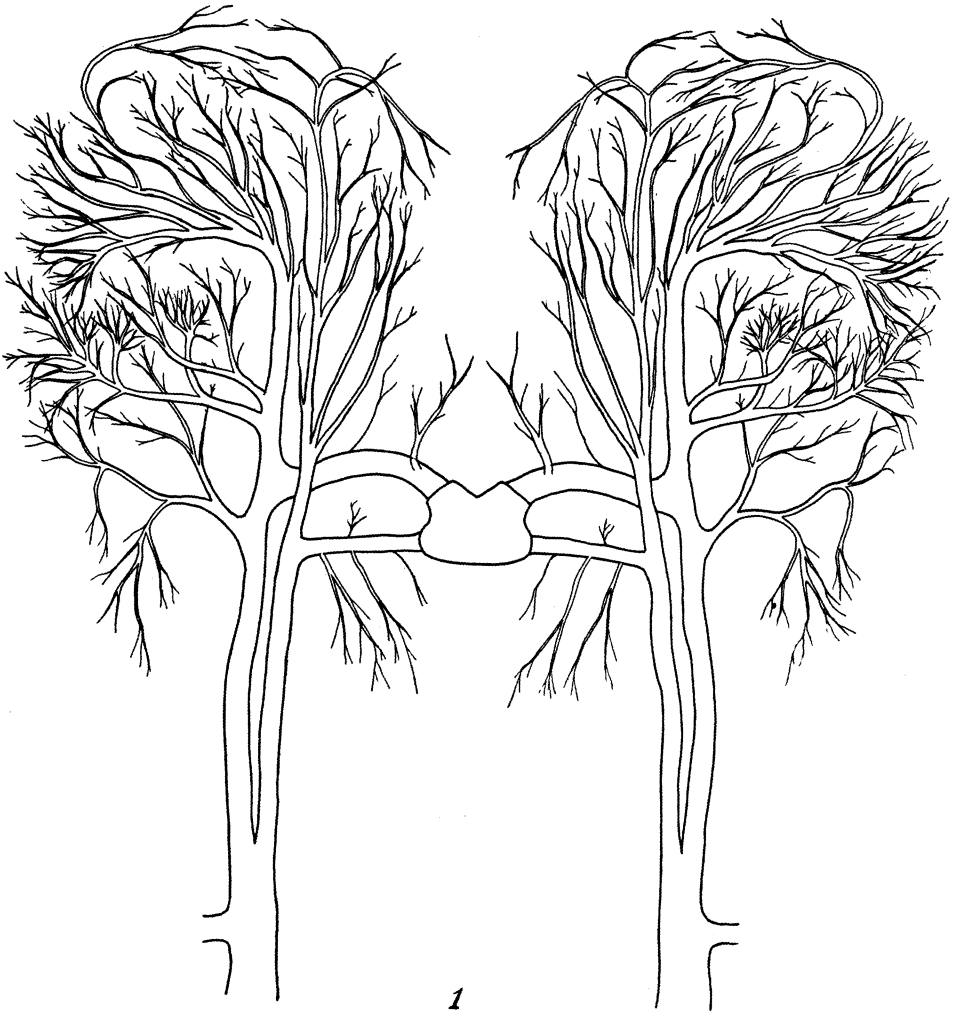
PLATE I.

All drawings (except Figs. 2 and 3) made with a camera-lucida. ×240.

FIG. 1. Palmen's organ in its relation to the tracheal system in the head of the nymph *H. interpunctata*. × 60.

FIG. 2. Sketch drawn from a specimen which had the organ removed and the four tracheæ broken off near their juncture with the main longitudinal tubes.

FIG. 3. Sketch drawn from a nymph in which the tracheæ were severed at their point of contact with the organ.



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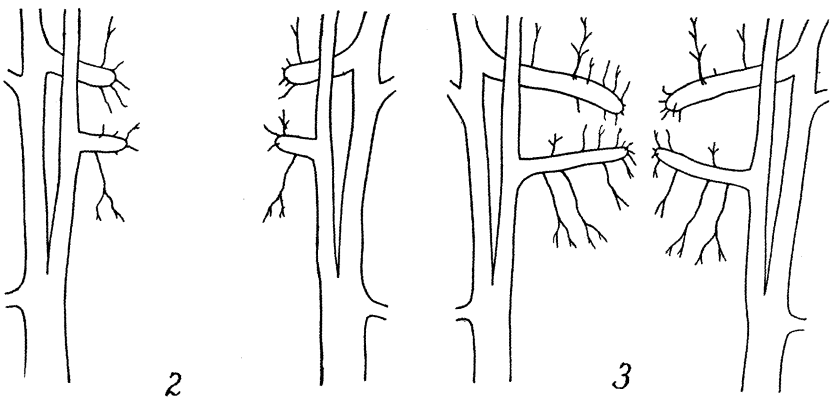

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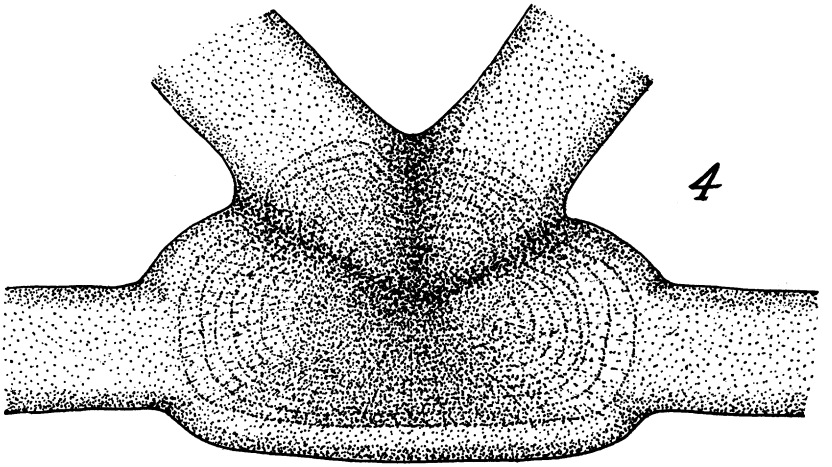
J. E. WODSEDALEK.

PLATE II.

FIG. 4. Representation of the entire organ surrounded by hypodermis, as it appears in a mounted specimen. Circular bands can be seen, especially at the edges of the organ, owing to the fact that we look at the vertical portion of each deeply colored part. In this view the large light areas appear at the entrances of the tracheal tubes; this is due to the fact that we look through a comparatively thin portion of the chitin in those regions owing to the direct extension of the cavities of the tubes into the organ. The darker areas appear as such because of their thickness; each is a concentric mass around the organ and forms the partition between the cavities.

FIG. 5. A horizontal section almost directly through the center of the two posterior tubes and a little above the center of the two anterior ones. It is only natural, therefore, that the two posterior tracheæ should lead to the solid central mass. The entrances of the two anterior ones are not in the same plane with that of the posterior pair and therefore the innermost portion of their cavities are not represented in this section. The gradually increasing diameter of each cavity is understood when we recall the development of the organ and the tubes leading to it.

FIG. 6. A horizontal section through the ventral projection of the organ which is apparent in Figs. 7 and 8. The central part of this figure appears clear because the section was quite thin and the cut parallel with the light portion of one of the concentric layers.



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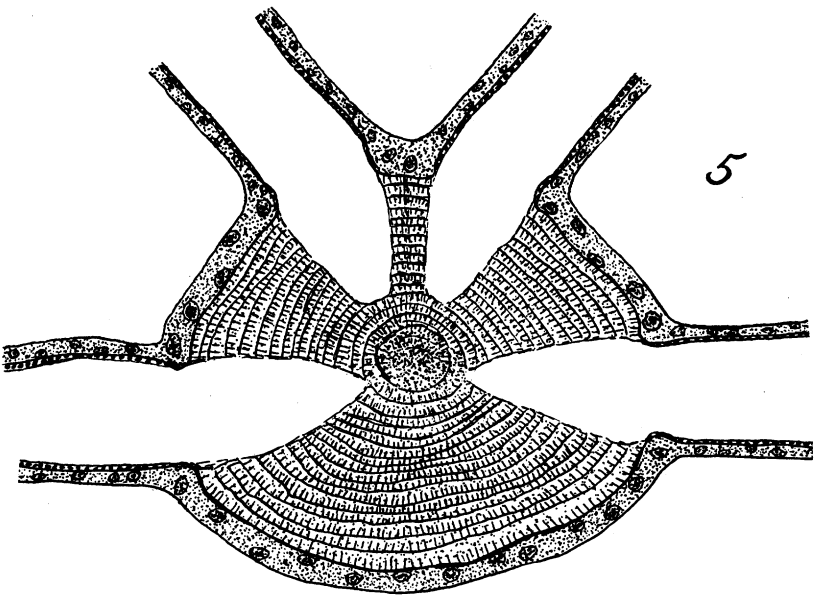

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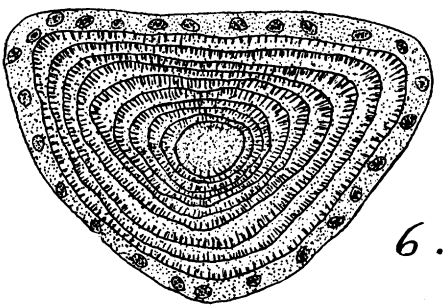


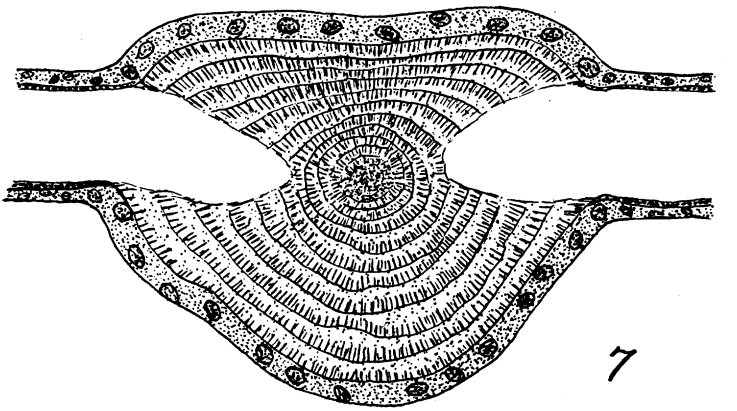
6.

PLATE III.

FIG. 7. A transverse section cut near the center of the posterior pair of cavities.

FIG. 8. An oblique transverse section cut through the front part of the posterior tube cavities and through the tips of the anterior cavities.

FIG. 9. A still more anterior view, only the cross sections of the two deeper portions of the anterior cavities being in evidence.



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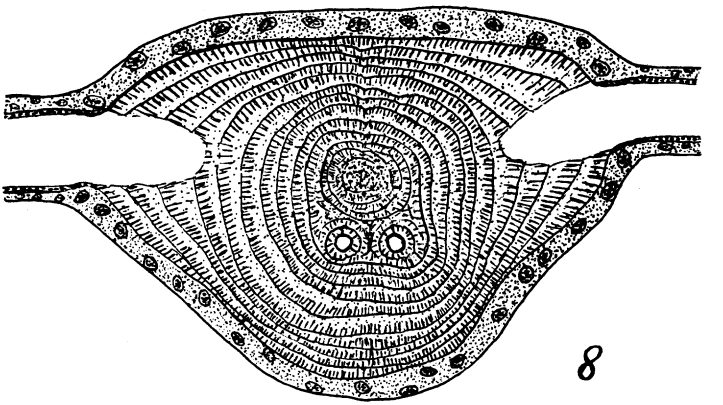

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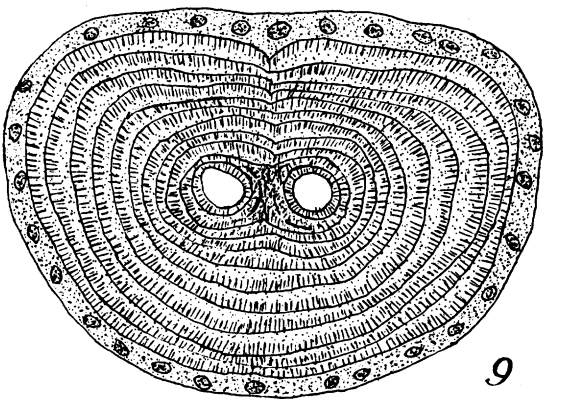

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J. E. WODSEDALEK.